

Aspects of variation in histology and cytology of the external nasal gland of Australian lizards

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Abstract

The histological and cytological structure of the external nasal gland was compared in 32 species of lizards representing the five families found in Australia. Considerable variation in the size of the gland was apparent, but size alone was not necessarily a reliable indicator of the gland's ability to function as an extrarenal salt-secreting organ. The elaboration of an hyperosmotic saline solution is associated with the presence of salt-transporting cells possessing a characteristic striated appearance, due to repeated folding of the basal and lateral membranes. These "striated cells" are generally grouped together into homogeneous tubular segments ("striated segments") which may occupy from 14% to 85% of the tubules in the gland depending upon the species. In the three large skinks studied, however, (*Egernia kingii*, *Tiliqua rugosa* and *T. occipitalis*) homogeneous "striated segments" do not occur, as salt-secreting and classical muco-serous cells intermingle throughout the length of the tubules and right up to the proximal end.

Nasal salt-secreting glands are most highly developed in the Australian Varanidae, and occur to some extent in all the Scincidae studied here. Salt-secreting elements occur rarely and then only feebly differentiated in the Australian Gekkonidae and Agamidae and are completely absent in the only member of the Pygopodidae examined, *Lialis burtonis*. External nasal glands in Australian lizards appear to differ from those described in species from both the Old and New World in that, even when apparently capable of functioning as salt-secreting glands, they show no obvious correlation with either environmental aridity or mode of nutrition.

Introduction

Recent studies have shown the lacertilian external nasal gland to be markedly polymorphic (Gabe & Saint Girons 1971, 1976; Dunson 1976; Lemire 1983). Often of small size and composed uniquely of classic glandular cells, it may also be enlarged and incorporate salt-secreting cells which are usually arranged in tubules having a characteristic striated appearance ("les segments striés" in the terminology of Gabe & Saint Girons, 1976). Although the mechanism of secretion is still not understood (Lemire 1983), it is clear that these cells are responsible for the capacity of these so-called "salt glands" to elaborate an hyperosmotic saline solution which, when eliminated, represents an important avenue of electrolyte excretion for many species. The presence and state of development of these salt-secreting cells appear to vary according to both the taxonomic position of the animal as well as its ecological situation.

From the literature it would appear that well-developed glands with striated segments are very common in the families Iguanidae and the Scincidae, frequent but more variable in their occurrence in the Varanidae, rare and very variable in their state of development in the Agamidae, absent or very little developed in the Gekkonidae and completely absent in the Chamaeleonidae and Anguioidea (including the Helodermatidae). By contrast, in agamids of the genus *Agama* and in the skink *Tiliqua rugosa* (Saint Girons, Lemire & Bradshaw 1977) the nasal gland is not

composed of typical homogeneous striated segments but, instead, salt-secreting cells are interspersed with classic glandular cells in the secretory tubules and are not restricted to an intermediary zone as in other species.

The ability of these glands to elaborate an hyperosmotic saline solution has been demonstrated unequivocally only in the case of the North African agamid lizard *Uromastix acanthinurus*, in about a dozen iguanids which are all herbivores and frequently desert-living or littoral species (see Lemire 1983 for references), and in three varanid species—one widely distributed in Australia (Green 1972), one littoral (Dunson 1974) and the other Saharan (Lemire 1983). In all the cases where the gland has been studied morphologically it is relatively large in size and packed with homogeneous striated segments representing from 65-95% of the total volume of the tubules.

Little is known of the physiology of "salt glands" from species where the gland is only moderately developed or where the salt-secreting elements form only 25-60% of the epithelium and the interpretation of data from such species is difficult (see Gerzelli & De Piceis-Polver 1970, Braysher 1971, Saint Girons *et al.* 1977, Minnich 1979). It does seem clear however that the small nasal gland of the Saharan *Agama* species has no osmoregulatory role, despite the fact that salt-secreting cells are common throughout the gland, intermixed with classical glandular cells (Lemire 1983). From a simple morphological point of view it is apparent that, within each Old World family, striated segments are more

common or more well-developed in species occupying arid regions and they are invariably highly developed in species which are primarily herbivorous.

The present investigation forms part of a detailed study of the ecophysiology of Australian reptiles, particularly lizards inhabiting arid and semi-arid regions of the continent (Bradshaw 1981, 1986) and an opportunity was taken to extend our limited knowledge of the morphology of these "salt glands" by examining common species living in a variety of habitats and representing the 5 families occurring in Australia.

MATERIALS AND METHODS

A list of the 32 species studied is given in Table 1. Amongst these, *Tiliqua rugosa* and the 4 varanids have already been the subject of detailed study (see Saint Girons *et al.* 1977, 1981). In the case of other species, specimens were autopsied the same day or the day following capture using Nembutal (Abbott, sodium pentobarbitone) as anaesthetic. The entire head was fixed for a period of 24 hr in aqueous Bouin, decalcified in 5% trichloroacetic acid, dehydrated and then blocked in paraffin. 10 μ m serial sections were reconstituted in 6

series by mounting one section in every 10 or 20, depending upon the thickness of the head. These series were then stained successively with PAS-haematoxylin-picro indigocarmine, Gabe's Single Trichrome and Azan for topographic studies and with Mowry's PAS-alcian blue to detect mucins and with Danicelli's tetrazoreaction for protids as described by Gabe (1976).

The volume of salt-secreting cells and striated segments, relative to either total cell volume or total secretory segments, and the relative size of the external nasal gland were estimated by eye following the method of Gabe & Saint Girons (1976). In addition, in those species where striated segments were quite distinct, photographs were made of the gland at three different levels, enlarged, and from these were cut all secretory segments both striated and glandular. These were then weighed to give an estimate of the relative proportion of salt-secreting to classical glandular portions of the gland. It should be emphasised, however, that it is possible to give a rough approximation only of the relative proportion of salt-secreting and classical glandular cells when both are interspersed all along the secretory tubules.

Table 1
List of species studied, habitat type and cytological and histological characteristics of the external nasal gland

Species	Habitat	Cell types		V1/V2*	Size of gland	Locality of capture of specimens
		C1	C2			
GEKKONIDAE						
<i>Crenodactylus ocellatus</i>	SA	MS	MS	0	2	NW W. Australia
<i>Diplodactylus stenodactylus</i>	SA	MS	MS	0	2	NW W. Australia
<i>Gehyra variegata</i>	A to H	MS	MS	0	2	Sydney
<i>Heteronotia binocet</i>	A to H	MS	MS	?	2	Alice Springs
<i>Oedura lesueuri</i>	SH	MS	MS	0	2	Sydney
<i>Rhynchoedura ornata</i>	A	MS	SM	0	2	NW W. Australia
<i>Underwoodisaurus milii</i>	M to SA	?	SM	0	2	Perth
PYGOPODIDAE						
<i>Lialis burtonis</i>	A to H	S	SM	0	3	Alice Springs
AGAMIDAE						
<i>Ctenophorus clayi</i>	A	SM	—	0	1	NW W. Australia
<i>Ctenophorus isolepis</i>	A	SM	—	0	1	NW W. Australia
<i>Ctenophorus maculatus</i>	SA	SM	—	0	1	NW W. Australia
<i>Ctenophorus ornatus</i>	M	SM	—	0	1	Perth
<i>Ctenophorus caudicinctus</i>	A	SM	—	0	1-2	NW W. Australia
<i>Ctenophorus nuchalis</i>	±A	SM	—	?	2	NW W. Australia
<i>Ctenophorus reticulatus</i>	±A	SM	—	?	2	Alice Springs
<i>Diporiphora australis</i>	H	SM	—	0	1	NE Queensland
<i>Lophognathus longirostris</i>	A	SM	—	0	1	Alice Springs
<i>Moloch horridus</i>	±A	SM	—	0	1	NW W. Australia
<i>Pogona minor</i>	A	SM	—	0	1	NW W. Australia
SCINCIDAE						
<i>Carlia fusca</i>	H	SM	MS	0.30	2-3	NE Queensland
<i>Carlia rhomboidalis</i>	H	SM	MS	0.38	2-3	NE Queensland
<i>Ctenotus taeniolatus</i>	H	SM	MS	0.32	2-3	NE Queensland
<i>Cryptoblepharus litoralis</i>	A to H	SM	MS	0.22	3	NE Queensland
<i>Egernia kingii</i>	M	MS	—	ca 0.3	2-3	Perth
<i>Hemiergis peronii</i>	M	SM	MS	0.47	2-3	Perth
<i>Menetia greyi</i>	±A	SM	MS	0.54	3	NW W. Australia
<i>Tiliqua occipitalis</i>	SA	MS	—	ca 0.3	2-3	NW W. Australia
<i>Tiliqua rugosa</i>	SA	MS	—	ca 0.3	2-3	Perth
VARANIDAE						
<i>Varanus giganteus</i>	A	SM	—	0.14	3	NW W. Australia
<i>Varanus rosenbergi</i>	M	SM	—	0.49	3-4	Perth
<i>Varanus acanthurus</i>	SA	SM	—	0.51	3-4	NW W. Australia
<i>Varanus gouldii</i>	A to H	MS	—	0.84	4	Perth

Habitat: A = very arid; \pm A = more-or-less arid; SA = semi-arid; M = Mediterranean; SH = semi-humid; H = humid. For C1 and C2 cells, type of secretion: S = serous; SM = sero-mucous; MS = muco-serous.

*V1/V2 = Ratio of volume of striated segments (or salt-secreting cells) to total tubular volume (or total glandular epithelium).

RESULTS

The general structure of the external nasal gland of lacertilians has been described on a number of occasions and excellent reviews will be found in Parsons (1970), Dunson (1976), Gabe & Saint Girons (1976) and Lemire (1983). Amongst the Australian species listed in Table 1 the epithelium of the glandular tubules is always composed, other than for small dispersed basal cells, of large cubic or prismatic cells (C1) with a basal nucleus and classified by their secretions as either *sero-mucous* (i.e. PAS-positive and rich in protids but without acid mucins) or *muco-serous* (i.e. PAS-positive and containing both protids and acid mucins). Rarely these C1 cells may be serous only, that is, rich in protids but PAS-negative and without acid mucins. In the Gekkonidae these cells are muco-serous but differ in being very weakly PAS-positive and staining with haematoxylin. In the Agamidae the secretory tubules are composed completely of C1 cells but, in other species, these cells which are always preponderant in the upper portions of the tubules, may be replaced progressively by other elements in the middle and lower reaches of the tubules.

A second category of cells (C2) which is very evident in the Gekkonidae and most of the Scincidae is composed of either muco-serous or (only in some Gekkota) sero-mucous cells, with a basal nucleus and PAS-positive secretions. In the upper (blind) parts of the secretory tubules these cells are small in size, conical in shape and compressed between the large C1 cells. In the middle section of the tubules the C2 cells enlarge progressively, assume a cubic or prismatic shape and become proportionately more numerous. In most of the Gekkonidae these are the only cell types to be found in the proximal section of the secretory tubules but in most of the Scincidae they appear to metamorphose into salt-secreting cells starting in the middle sections of the tubules.

In the three large skinks (*Egernia kingii*, *Tiliqua rugosa* and *Tiliqua occipitalis*) and all the varanids, the small conical cells in the upper regions of the tubules (C2?) lack secretory products and their progressive transformation into salt-secreting cells is more evident. Once well-differentiated, these cells appear pyramidal or prismatic with a central clear ovoid nucleus and with a cytoplasm completely devoid of secretory material but filled with mitochondria. The extreme folding of the lateral cellular membranes, and often the basal membrane as well, confers on the epithelium of these cells a characteristic striated appearance when viewed under the light microscope (les "cellules striées" of Gabe & Saint Girons, 1976). In a more-or-less long transition zone, near the blind end of the secretory tubules, these salt-secreting cells in the process of differentiation are mixed with C1 cells. In the proximal section of the tubules the completely formed salt-secreting cells produce homogeneous striated segments in the Varanidae and *Menetia greyi*. In most of the Scincidae one can still talk of "striated segments", even though some C1 cells will be found in the epithelium, but in the three large skinks, salt-secreting cells and muco-serous cells intermingle right up to the proximal end of the secretory tubules, even though the salt-secreting cells become progressively more abundant.

In some cases the cellular composition of the epithelium is difficult to define precisely, at least under the light microscope, because of the gradual differentiation of the salt-secreting cells. In *Ctenophorus nuchalis* and *Ctenophorus reticulatus*, for example, the

muco-serous cells (C1) become taller with clearer nuclei sited further from the basal membrane in the proximal third of the secretory tubules, and their secretory products become less evident and finally disappear altogether so that the striated aspect of the epithelium is not at all clear. The same phenomenon, although a little less obvious, is also seen with *Ctenophorus caudicinctus*, and in *Heteronotia binocci* an analogous situation is seen in the proximal portion of the tubules.

Given the wide variations in head shape and nasal cavities from one Family to another, and even between related genera, it is difficult to arrive at precise figures for the relative volume of the external nasal gland in different species and this is further complicated by variations in the proportion of glandular tubules to conjunctiva. Gross comparisons are nevertheless possible, and the relative development of the gland is given for each species in Table 1 on an arbitrary scale from 1 to 4 with 1 being represented by most of the agamid species and 4 by *Varanus gouldii* which has an active salt-secreting gland.

DISCUSSION

The aim of this investigation was twofold: firstly to extend our very limited knowledge of the histological structure of the external nasal gland of Australian lizards and, secondly, to document variations in the relative abundance of salt-secreting elements in the glands of these lizards and to correlate these wherever possible with differences in ecology, geographic distribution or systematic position of the species concerned.

Our results confirm those of other workers and salt-secreting cells were found in all Scincidae; "striated segments" occurred frequently but showed variable development in the Varanidae and they occurred rarely and then were only feebly differentiated in the Gekkonidae and in most of the Agamidae. Striated segments were completely absent from the external nasal gland of the only member of the family Pygopodidae included here, *Lialis burtonis*. Taking into account the relative development of the salt-secreting cells, whether or not assembled into homogeneous striated segments, the lizards studied here fall into three separate groups. The first is represented by *Varanus gouldii* where striated segments constitute the major part of the gland (see also Saint Girons *et al.* 1981); the second by various Varanidae and Scincidae which all possess clearly-developed striated segments or numerous salt-secreting cells interspersed with classic glandular cells ("mixed" glands); and the third by the geckos, agamids and the pygopodids where salt-secreting cells are either absent or very rare and poorly differentiated when they do occur.

Within the Scincidae it is possible to distinguish a further three distinct groups according to the distribution of the salt-secreting cells within the gland. In *Scincus scincus* (Lemire 1983), *Chalcides mionecton* (Gabe & Saint Girons 1976) and *Menetia greyi*, which are all semi-fossorial species from more-or-less arid regions, there are two categories of classic glandular cells in the distal regions of the secretory tubules, whereas the middle and proximal regions are occupied by voluminous and homogeneous striated segments. Most of the Australian skinks fall into a second category which conforms essentially to this basic pattern but differs in a slightly lesser development of the striated segments and the fact that the muco-serous C2 cells occur scattered throughout the epithelium, right up to the level of the excretory duct. The third group is represented by the



Figure 1.—Transverse section of the head of *Varanus acanthurus* at the level of the external nasal gland. Stained with PAS-haematoxylin-picro-indigocarmine, green filter x 50. "Striated segments" which are more voluminous and lack secretory products are indicated by arrows and are quite distinct from the classical glandular secretory elements.

three large skinks studied here (*Tiliqua rugosa*, *Egernia kingii* and *Tiliqua occipitalis*) where it is clear that even though the maturation of C2 cells into salt-secreting cells commences in the distal regions of the secretory tubules, homogeneous striated segments are never formed because C1 cells can still be found at the proximal extremity of the tubules. In contrast, the external nasal gland of the Australian agamids, although equally poorly developed, differs from that of the Saharan *Agama* (Lemire 1983) in that there is never a mixture of classical glandular cells and salt-secreting cells within the one tubule, and when the former develop into salt-secreting cells, they do so incompletely and only at the proximal extremities of the secretory tubules.

Cytological components associated with salt secretion assume an important proportion of the glandular tubules only when the nasal gland is well developed (2 in our classification) but large nasal glands are not necessarily dedicated to salt-secretion. In *Lialis burtonis*, for example, the external nasal gland is well developed (3) but contains no salt-secreting cells whatsoever. This highlights the difficulty experienced by many workers (ourselves included) in attempting to gauge the physiological potentialities of a given gland from its histological structure. There is no doubt that *Varanus gouldii*, which possesses a voluminous external nasal gland composed primarily of homogeneous striated segments, has the capability of elaborating an hyperosmotic saline solution and this has been

confirmed experimentally by Green (1972). It is highly probable that this same capacity is also shared by other lizards falling in the second group, such as *Menetia greyi*, *Varanus acanthurus*, *Varanus rosenbergi* and *Hemiergis peronii*, all of which live in arid and semi-arid regions throughout Australia. *Varanus gouldii* is distributed throughout the entire Australian continent and is found in desert as well as sub-humid forest situations but it is not known whether the nasal gland is equally developed in all individuals. Typically, the individuals which have been studied come from arid or semi-arid situations where one would expect, *a priori*, the gland to be well developed, and Green's animals (*op.cit.*) for example were collected in arid regions of South Australia. *Varanus rosenbergi* is more mediterranean in its distribution but is often found in littoral situations where salt intake would be expected to be elevated.

It is difficult to predict in the case of those other species falling in this second category—possessing salt-secreting cells either dispersed throughout the gland or forming almost homogeneous striated segments, but accounting for only 10-40% of the total volume of the secretory tubules—whether their nasal glands are capable of secreting an hyperosmotic solution. At least in the case of the skink *Tiliqua rugosa* which possesses such a "mixed" gland, it is clear from recent work by Bradshaw, Tom & Bunn (1984) that this lizard is capable of elaborating such a solution in response to electrolyte

loading with either NaCl or KCl and the fluid excreted from the gland has an osmotic pressure approximately 3.5 times that of the plasma. Further studies are needed urgently, however, in order to define the physiological capacities of these glands which, at first sight, would seem to lack the requisite development and organisation of salt-secreting elements required to elaborate a concentrated salt solution (Saint Girons *et al.* 1977).

When one looks for correlations between the development of the external nasal gland in the various species included in this study and their geographic distribution within Australia, none emerges. For example, the nasal gland of *Carlia rhomboidalis* is well developed with obvious striated segments and would appear, on histological criteria, capable of secreting a hypersaline fluid, but this species is localised in one of the wettest regions of Australia where it would not be expected to have any need of an extra-renal salt-secreting organ. *Varanus giganteus* on the other hand is found exclusively in the most arid regions of the continent and yet possesses a nasal gland in which striated segments are only very poorly developed and it would appear that, within Australia at least, nasal salt glands bear little correlation with environmental aridity. The other correlation noted in reptiles from both the Old and New World is herbivory, but none of the Australian lizards is an obligate herbivore, like for example the North African agamid *Uromastix acanthinurus*. The three large skinks studied here, which are all partially herbivorous (*Tiliqua rugosa*, *Tiliqua occipitalis* and *Egernia kingii*) show no greater development of salt-secreting elements in their external nasal glands than do insectivorous species.

Given the morphology of the external nasal glands of lizards falling in the third category, where salt-secreting cells are either absent or only marginally developed, any role of the gland in osmoregulation can be excluded. This includes all the species of the genus *Ctenophorus* studied, many of which live in particularly arid regions. This is consistent with what is known of the water and electrolyte physiology of these lizards which survive long periods of water deprivation through their ability to retain sodium ions in the body fluids at markedly elevated concentrations (Bradshaw & Shoemaker 1967, Bradshaw 1981, 1986). Lizards of the genus *Agama* living in the Sahara similarly tolerate hypernatraemia, rather than excrete sodium ions via an external nasal gland (Lemire 1983) and even *Uromastix acanthinurus*, which possesses one of the most developed external nasal glands of any lizard, has a very limited ability to excrete sodium ions as shown by the work of Bradshaw *et al.* (1984) and experiences hypernatraemia in its natural habitat during periods of water deprivation (Lemire *et al.* 1982). Amongst the *Ctenophorus* species examined here, only *caudicinctus* and *nuchalis* show any tendency towards development of salt-secreting cells in the nasal gland, as with *Heteronotia binoei* amongst the geckos. The ecological and physiological significance of this is, however, obscure, particularly in the case of this gecko which has recently been shown to be parthenogenetic in parts of its range (Moritz 1983, 1984).

In conclusion, it would appear that ecological and environmental correlates with nasal gland development, particularly aridity and mode of nutrition, are much less obvious in Australian lizards than in other parts of the world. In part this may stem from our poorer knowledge of the ecology of many of these species and it would be most useful for future ecophysiological studies if the osmoregulatory capacities of these glands could be defined.

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